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Distribution: Temperate China, East Himalayas and Japan.

Baltimore, Maryland.

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REVIEW

A study of the genus Paeonia. By F. C. STERN. London, Royal Horticultural Society. viii + 155 pp., 15 colored plates, 28 text figures, 8 maps. 1946. 63s.

There is probably no group of non-professional botanists to whom plant science owes a greater debt than the botanical and horticultural enthusiasts of Great Britain. Their energy in gathering together collections of both specimens and living plants from all corners of the earth, their care in raising a great variety of rare, exotic, and "difficult" species in their gardens, and their generosity in financing the explorations and research studies of their friends in the professional field of botany has widened immensely our knowledge of the world's flora. And their standards of execution have been consistently high, both as to the accuracy of the research and the elegance of the publication. Consequently it is more of a pleasure than a surprise to learn that during Britain's "darkest hour" of the last war there was being prepared a botanical work which is not only a fitting successor to its great array of predecessors, but which in addition is in many ways a model for progressive monographic studies of the future.

Mr. F. C. Stern's work on *Paeonia,* modestly entitled a "study," is actually a magnificent folio volume, superbly illustrated with accurate and highly artistic color plates of most of the species, supplemented by line drawings of some of the technical details and a complete set of distributional maps. The technical portions of the monographic treatment; nomenclatural history, synonymy, species descriptions, and discussions of diagnostic morphological characters, are full and accurate. The artificial key to the species is concise and as easy to follow as one can make it in a genus like *Paeonia,* which simply does not have the clear cut diagnostic characters found in many other groups. Most of the species descriptions are accompanied by helpful and well written accounts of the appearance of the living plants and of the proper methods of culture. Mr. Stern has shown that he is not an amateur in any sense of the word which refers to his degree of competence, but that in regard to its literal meaning he is a true lover of the plants to which he has devoted so much of his life.

But even more interesting than these parts of the work are the sections on the cytology and distribution of the species. The chromosome numbers are given of 34 of the 47 species, varieties, and forms; of the 13 not listed, 8 are poorly differentiated varieties of species of which the number is known, 2 are members of the tetraploid *mascula* and *officinalis* complexes, and undoubtedly have the same numbers as their close relatives; and the remaining three are the rare *P. kesrouanensis,* native to Syria, and two closely related endemics of southwestern China, *P. Mairei* and *P. oxypetala. Paeonia* thus ranks with *Crepis, Nicotiana,* and *Gossypium* as one of the best known cytologically of plant genera. The species are all either diploids with the somatic number $2n = 10$, or tetraploids with $2n = 20$.

The patterns of distribution of the various species provide material for a most interesting discussion. Endemism is common in the genus; 8 of the 33 recognized species are restricted to a single island, mountain range, or other small area. The genus as a whole occurs in five disjunct areas; the Mediterranean region; central Asia from the Urals to Siberia with an outlier in eastern Lapland; the western Himalaya; eastern Asia from southwestern China to Manchuria and Japan; and Pacific North America. Such a distribution is evidence of the great age of the genus, as is also the primitive nature of its morphological characteristics. Stern points out that the cytological condition of the species is characteristic for each separate area of distribution. North America contains only two diploid species, which have a distinctive type of chromosome behavior at meiosis. The species of eastern Asia are diploid with one exception, while those of Central Asia and the Himalaya are strictly diploid. The Mediterranean species include both diploids and tetraploids, with the latter having by far the widest distributions. This latter fact brings forth a very plausible hypothesis as to the origin of these tetraploids. The diploid species are believed to be preglacial relics, which were pushed southward by the advancing ice sheet of the Pleistocene period, and took refuge in the islands of the Mediterranean and other warm areas. The tetraploids, which are believed to have arisen from the diploids by autopolyploidy, were supposedly the only forms which were able to migrate northwards in postglacial times.

There are probably few genera about which two botanists, studying the species independently and with different materials available, would agree completely as to the true relationships and boundaries of the species. *Paeonia* is no exception. The writer has spent some time studying this genus, his work being based largely on the living plants and interspecific hybrids kindly made available to him by Dr. A. P. Saunders of Clinton, New York, but supplemented by inspection of nearly all of the specimens available in American herbaria. His synopsis (Univ. Calif. Publ. Bot. 19: 245–266. 1939) differs in some respects from the arrangement of the species as given by Stern, and the evidence presented in Mr. Stern's study has not been sufficient to persuade him to change more than a few of his concepts, except in the case of names which must be altered for nomenclatural reasons.

In the first place, Mr. Stern's concept of the species is entirely morphological, and based chiefly on the ease with which they can be recognized in herbarium specimens. The present writer concluded that the three sets of characters which most sharply set off the majority of the species are those of the sepals, the carpels and stigmas at anthesis, and the mature seeds. Since, as Mr. Stern states, none of these can be readily studied in herbarium specimens, they are not included in either his key or the species descriptions. In the writer's decisions as to which forms should be recognized as species and which as subspecies, the ability of forms to cross in the garden and form fertile hybrids played an important role, particularly if the types concerned were known to occur naturally in the same or adjacent regions. Mr. Stern refers in some instances to the observation of the writer and Dr. Saunders that certain types hybridize freely in the garden, but fails to mention the significant fact that in those instances where the genetic evidence caused the writer to group different forms into the same species, as in *P. Delavayi, P. lutea,* and *P. Potanini;* and in *P. daurica* ("*P. triternata*") and *P. Mlokosewitschii;* the hybrids formed were fully fertile. Some valid species, like *P. Veitchi* and *P. Emodi,* as well as *P. daurica* and *P. tenuifolia,* also hybridize easily, but produce almost completely sterile F_1 hybrids characterized by very irregular meiosis. On the other hand Mr. Stern places in the same species as the yellow flowered *P. Wittmaniana* the plant from the Caucasus first believed by Dr. Saunders and the writer to be *P. macrophylla* and later *P. tomentosa.* This plant has white, not yellow flowers; its sepals and petals are much broader than those of *P. Wittmaniana,* and the shape of the sepals is entirely different; its carpels are not only tomentose, but both the shape of the carpels and that of the stigmas is entirely different from those of the yellow flowered form recognized by Stern as *P. Wittmaniana* var. *nudicarpa.* Furthermore, the hybrid between these two forms is completely sterile. In every respect they appear to the writer far more distinct than such species as *P. arietina* and *P. officinalis,* which Stern places in different subsections of the genus, but which are able to form fully fertile hybrids.

Considerations like these cast considerable doubt on the validity of the two subsections recognized by Stern in the section (or subgenus) *Paeon,* namely *Foliolatae* and *Dissectifoliae.* They are in general distinct and natural groupings, but exceptions to this situation exist in the species groups of *P. officinalis, P. peregrina,* and *P. arietina,* all of them tetraploid, and admittedly by far the most difficult species groups in the genus. Mr. Stern has done a great service in describing the characteristics of leaf morphology by which their "species" may be identified, and in stating clearly their geographic distributions. But his evidence that they occur in adjacent areas rather than together in the same region, and that in at least some instances they intergrade where their ranges overlap, suggests to the present writer that they represent members of a typical "Rassenkreis" or polytypic species as recognized by zoologists, and that each of Mr. Stern's "species," in these three groups, with the exception of the more distinct and cytologically diploid *P. Clusii,* is a typical geographic subspecies. This point of view is supported by the hybridization experiments of Dr. Saunders.

That these differences of opinion in regard to the limits of species are not purely academic is evidenced by the fact that Mr. Stern and the writer hold opposite points of view in regard to the nature and origin of the tetraploids. His hypothesis that they arose and spread in response to the climatic changes which took place during the Pleistocene epoch is entirely plausible, but the belief that each tetraploid species arose separately and independently as an autotetraploid from a different diploid species is not in accord with a number of facts. In the first place, many of the tetraploids could, on morphological grounds, be just as easily connected with an entirely different diploid species from the one chosen by Mr. Stern. For instance, a comparison of the illustrations in Mr. Stern's study suggests that *P. Russi,* which he relates to *P. Cambessedesii,* is in many respects like *P. Broteri,* and could be derived from that species almost as easily, and study of details of floral structure supports this view. *P. mascula,* which is considered to be derived from *P. daurica,* is in many respects equally similar to *P. Cambessedesii* and *P. Broteri,* and Stern remarks (p. 68) that "the form of *P. mascula* in Sicily looks very like *P. Russi* when examined as dried specimens." *P. banatica,* which such botanists as Kitaibel, and Ascherson and Graebner have considered to be a variety of *P. officinalis,* is regarded by Mr. Stern as derived from *P. mascula,* and so indirectly by autotetraploidy from *P. daurica.* But in the descriptive section he states (p. 72): "It is difficult to say whether this plant may be a variety of *P. mascula* or of *P. arietina,* since it has some of the characters of both of these paeonies." *P. arietina* is believed to be an autopolyploid from *P. rhodia,* a species very different from *P. daurica.* Finally, Mr. Stern considers that the two genetically isolated species grouped by him under *P. Wittmaniana* are autopolyploids of *P. Mlokosewitschii.* But although *P. daurica* and *P. Mlokosewitschii* are interfertile and differ in nothing except flower color and leaf shape, their two supposed autotetraploids, *P. mascula* and *P. Wittmaniana* (including *P. tomentosa*) are widely divergent in a number of morphological characteristics, and would almost certainly form highly sterile hybrids if intercrossed.

All of these facts support the writer's belief that the tetraploid peonies of the Mediterranean region form a typical polyploid complex, in which autopolyploidy has figured to a certain extent, but of which the majority of the species are allopolyploids derived from crossing between either the present day diploids or their ancestors or autopolyploid forms. Those belonging to the subsection *Foliolatae* are derived from the diploids of this subsection, *P. Cambessedesii, P. Broteri, P. rhodia,* and *P. daurica.* But the tetraploid *Dissectifoliae,* namely *P. officinalis* and its relatives, probably represent ancient allopolyploids involving on the one hand Mediterranean diploids, like *P. Clusii, P. rhodia,* and *P. daurica,* and on the other, the central Asiatic *P. anomala.* The best morphological evidence for this hypothesis lies in the appearance of *P. peregrina,* the most easterly of these tetraploids, which is one of the two species for which Mr. Stern could not find a diploid ancestor. But *P. officinalis,* which Mr. Stern believes to be an autotetraploid of *P. Clusii,* differs from the latter species in its relatively narrow leaves, while the most common effect of autopolyploidy on leaf shape in dicotyledons is to make the leaves shorter and broader. The influence of *P. anomala,* which has narrow as well as strongly lobed leaflets, would tend to produce precisely the divergence in leaf shape which is found in *P. officinalis* and *P. peregrina* as compared to *P. Clusii.* Furthermore, these tetraploids have one leaf characteristic not observed by Mr. Stern which is characteristic of *P. anomala* and its relatives, but is not found in any of the Mediterranean diploids, including *P. Clusii;* namely the presence of short, scabrous pubescence along the veins of the upper surface of the leaf. Finally, the hybrids produced by Dr. Saunders between *P. Mlokosewitschii* and *P. anomala* as well as *P.*

Veitchii resemble closely members of the *P. officinalis* complex in all of their features of external morphology.

The cytological evidence, also, supports the present writer's hypothesis. In the species of *Paeonia,* with their large chromosomes and random distribution of chiasmata, a high proportion of multivalents is to be expected if the component genomes of a tetraploid are completely homologous, or even if they are not quite so. But in most of the tetraploids investigated by the writer and Mr. S. O. S. Dark (Jour. Genetics 32: 353–372) including *P. officinalis, P. peregrina,* and *P. Wittmaniana,* the number of quadrivalent configurations per nucleus is only one or two, with most of the chromosomes paired as bivalents. This would suggest that the four component genomes of these tetraploids are not completely homologous, and that they belong to the category recently characterized by the writer (Advances in Genetics 1: pp. 417–421) as segmental allopolyploids, or polyploids of which the component genomes bear the majority of their chromosomal segments in common, but in which these genomes differ from each other by a large enough number of such segments so that free interchange between them is barred by complete sterility on the diploid level. The fact that most diploid inter-specific hybrids of *Paeonia* may form as many as four or five bivalents suggests that polyploids derived from them would be of this nature.

The hypothesis that the members of the *P. officinalis* complex arose as allotetraploids from hybrids between the Mediterranean diploids and *P. anomala* presupposes that at the time when these hybridizations took place the distributions of the diploid species were very different from what they are now. But both Mr. Stern and the writer are agreed that the present Mediterranean diploids are relics which had a considerably wider distribution before the beginning of the Pleistocene ice age. And fossil remains of late Tertiary age from western Europe, particularly the abundant seeds collected by Reid and Reid in the Pliocene deposits of the lower Rhine basin, contain a large proportion of species of flowering plants now confined to Asia, indicating the presence of a strong Asiatic element in the European flora at that time, which might easily have included *Paeonia anomala* or a relative of that species. The writer, therefore, would like to modify Mr. Stern's hypothesis in regard to the origin and evolution of the tetraploid species of *Paeonia,* and believes that they originated through a series of hybridizations between diploid species or their autotetraploid derivatives. The first of these hybridizations took place not later than the middle or end of the Pliocene epoch, but the process very likely was continued during the interglacial periods of the Pleistocene. The tetraploids have persisted and spread not only because of such beneficial qualities as might have been given them by their increased chromosome number, but also, and perhaps chiefly because they possess favorable combinations of genes derived from ecologically as well as morphologically different ancestral species, which gives them a relatively wide range of tolerance of diverse ecological conditions.

The final decision as to the correctness of one or the other of these hypotheses, as well as to the validity of the writer's species concepts insofar as they differ from those of Mr. Stern, cannot be made through any attempt to improve on Mr. Stern's fine monographic study by means of examining further the herbarium specimens and garden plants now available to us. Careful studies are needed of the critical species as they grow in nature, and the splendid series of interspecific hybrids produced by Dr. A. P. Saunders needs to be increased and studied more carefully. Unfortunately the present state of the world makes both of these types of studies seem like remote ideals rather than actualities for the immediate future. Such parts of the globe as Dalmatia, Greece, Syria, and the Caucasus are considered by most people at present to be critical areas for very different reasons from the fact that those regions will yield important information about the relationship of ***Paeonia*** species. And the years of labor and devotion expended by Dr. Saunders on his beautiful creations are a scarce commodity in this age of fear, hurry, and utilitarianism. But peonies have existed on this earth for many millions of years, and they will still be with us when the world settles down to a more normal way of living. And when that time comes, Mr. Stern's "study" may be looked upon as one of the outstanding achievements of the present period in the history of plant science. —G. L. Stebbins, Jr., University of California, Berkeley, California.

NOTES AND NEWS

Range Extensions of Grasses into Colorado.[1] In connection with the preparation of a flora of Colorado many plants not listed for the state in the various manuals and monographs have come to light. Among these unrecorded plants are 32 grass species.

Because of the great economic importance of the grass family in this region, and because, as far as can be ascertained, the majority of these grasses are a part of the actual flora of the state, it was considered worth while to put them on record, together with the herbaria wherein the specimens are deposited. The following abbreviations are used: University of Colorado (CU); Colorado Agricultural and Mechanical College (CA); Colorado College (CC); United States Forest Service, Regional Office, Denver (FS); Rocky Mountain Forest and Range Experiment Station, Fort Collins (FES); private herbarium of Paul Ginter, Fort Collins (G); Soil Conservation Service, maintained by the Department of Range and Pasture Management, Colorado Agricultural and Mechanical College (SS); United States National

[1] Scientific Series Paper 216, Colorado Agricultural Experiment Station.